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The observations of the writer on the enormous variability of the F_2 generations arising from partially sterile F_1 generations produced by crossing species, led him to suspect that such combinations might be the basis of a great deal of variability responsible for evolution under domestication. A careful survey of the evidence relating to the origin of modern horses, cattle, sheep, swine, dogs, guinea pigs, fowls, ducks, and geese on the one hand, and varieties of wheat, corn, barley, oats, rye, apples, grapes, roses and begonias on the other hand, shows that in every case several related wild or semi-wild species exist which will cross together and yield partially fertile offspring. Doubtless many other species which have shown great improvement under domestication, would be found to have wild relatives which behave similarly, should they be investigated. Both the historical and the experimental evidence, therefore, point to hybridization, and particularly to species of hybridization, as the great single cause of evolution under domestication.

At the same time, one must not confuse evolution under domestication with natural evolution. The outstanding biological feature characteristic of the varied groups of domestic animals and of cultivated plants, is the perfect fertility within each group. A marked peculiarity of the great majority of natural species is their sterility with one another, the origin of which has long been a stumbling block to writers on evolutionary biology. Our own experimental evidence, as far as it goes, and observations on domestic forms which presumably have originated from combinations of two or more wild species, yield not the slightest indication of a tendency toward the production of segregates that exhibit either incompatibility in crosses or sterility of the individuals produced by hybridization.

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THE MEASUREMENT OF LINKAGE

LINKAGE is a name for that tendency sometimes shown by genes to maintain in hereditary transmission their previous relations to each other. Thus if two linked genes, A and B, enter a cross together, in the same gamete, they will oftener than not be found together in the gametes formed by the cross-bred individual. And if the same two genes enter the cross separately,

one in the egg, the other in the sperm, then oftener than not they will be found apart, in different gametes formed by the cross-bred individual.

Where no linkage exists between two genes, A and B, it will be wholly a matter of chance whether they go together or not, no matter what their previous relation was. We say that they "assort independently," as genes do in ordinary Mendelian inheritance, such as was known to Mendel. In such cases change of relation occurs in the long run in half (or 50 per cent.) of all cases. Such change of relation is called "crossing over." Linkage evidently will be shown by a falling below 50 in the percentage of cross-overs. The more cross-overs decline below 50 per cent., the stronger will be the linkage indicated, until when no cross-overs occur, we call the linkage complete or perfect. Accordingly 0 and 50 per cent. will be the limiting values for cross-overs indicating linkage. But it is conceivable that cross-overs might occur in excess of 50 per cent. What would their significance be? Not linkage, not a tendency to maintain relations previously existing between genes, but a tendency to *change* those relations, to go apart when previously together, and to get together when previously apart. We are not acquainted with any such tendencies as these, and it is difficult to imagine how they might arise, but it is certain that they would be the opposite of linkage and would need a different name, if observed.

It is evident that the strength of linkage increases, as the cross-over percentage decreases below 50. As a measure of the strength of linkage, we might then take the difference between 50 and the observed cross-over percentage, as I have elsewhere suggested (Castle, 1919). This would give us a numerical grade of linkage strength on a scale of 50. But since we are more accustomed to grading on a scale of 100, it will perhaps be better to double values thus obtained. Our grading scale of linkage strengths will then run thus:

Cross-over Percentage	Linkage Strength
50	0
40	20
30	40
20	60
10	80
0	100

By this method we can compare the linkage strength between

any two pairs of genes without stopping to reverse the relations indicated by cross-over percentages. For example the following linkage relations are shown by the genes of rats and mice (Dunn).

Genes	Cross-over Percentage	Linkage Strength
Albinism—red-eye, rats	1.8(?)	96.4
Red-eye—pink-eye, rats	18.3	63.4
Albinism—pink-eye, rats	21.1(?)	57.8
Albinism—pink-eye, mice	14.6	70.8

The strongest linkage here indicated is that between albinism and red-eye in rats, next comes that between albinism and pink-eye in mice. But albinism and pink-eye in rats show less linkage than in mice. The three genes, albinism (*c*), red-eye (*r*) and pink-eye (*p*) in rats are apparently arranged in linear fashion thus:

c.....r.....p
0 2(?) 21

This kind of a diagram is what Morgan, Bridges and Sturtevant (1919) have made familiar to us under the name of "chromosome map." Not to prejudice the case for or against the chromosomes, we might perhaps call it a linkage map or map of a linkage system. In its construction we use cross-over percentages as direct measures of map distances, but in *Drosophila* at least only distances relatively short have been found to be strictly comparable. Beyond distances of about 5 units (cross-over percentages) it is found that double or triple cross-overs become increasingly common and thus decrease the apparent number of breaks in the linkage chain between two genes. So that long map distances are based, not on directly observed cross-over percentages between the more distant genes, but on summation of intervening short distances, it being assumed that the arrangement is in all cases linear. While this latter assumption is not to be accepted for all cases without proof, it must be admitted that for *Drosophila* at least the evidence for a linear arrangement is very strong and no insuperable objections can be raised against it.

Map-distances have been found in the "first chromosome" linkage group of *Drosophila* exceeding 60, and in the "second chromosome" group exceeding 100. But in no case does the observed cross-over percentage between two genes, however remote, of the same linkage group exceed 50. This means that

beyond very short distances cross-over percentages do not increase in proportion to distance. The linkage group forms a means of holding genes together, however distant they may be from each other, so that, as one goes, all have a tendency to go. The linkage map will give us a diagrammatic view of the relations to each other of the genes composing a linkage system. It is based on the *shorter observed cross-over percentages*, or where longer distances are used, they must be first corrected for double and triple crossing-over. See in this connection the valuable Table II. of Haldane (1919) which provides a ready means of converting map distances into cross-over percentages or *vice versa*, and so of predicting undetermined linkage relations. It is based on a mathematical examination of the linkage system of the first chromosome of *Drosophila*. A table of linkage strengths will show us, without reference to distances involved, to what extent the movements in gametogenesis of one gene are correlated with those of any other gene. It is based on the *unmodified cross-over percentages observed*, whether the map distances involved are great or small. Linkage strengths can never exceed 50 on a scale of 50, 100 on a scale of 100, whereas map-distances may be extended indefinitely with the discovery of new genes.

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IS THERE LINKAGE BETWEEN THE GENES FOR YELLOW AND FOR BLACK IN MICE?

IN a recent number of this journal Dunn¹ has given data showing a deficiency of black young in a family of yellow mice.

¹ AM. NAT., 53: 558-560, 1919.